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9th JUly 2014

Re: Multi-authored Comment on Grellet-Tinner and Codrea (2014)

Dear Editors, Prof Santosh:

Following our extensive correspondence over email, please find our submitted Comment on the recent Grellet-Tinner and Codrea (2014) article in GR: "Thalassodromeus sebesensis, an out of place and out of time Gondwanan tapejarid pterosaur", Grellet-Tinner and Codrea (online July 2014 DOI 10.1016/j.gr.2014.06.002)

I did not see the Comment and Reply format for submission to the Journal (on this site) so have used the GR Letter submission format; I hope that is ok for review.

Yours sincerely

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Thalassodromeus sebesensis - a new name for an old turtle. Comment on "*Thalassodromeus sebesensis*, an out of place and out of time Gondwanan tapejarid pterosaur", Grellet-Tinner and Codrea (online July 2014 DOI 10.1016/j.gr.2014.06.002)

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1. Introduction

In a recent *Gondwana Research* article Grellet-Tinner and Codrea (2014) (hereafter "GTC") describe a single bone (UBB ODA-28, collections of Babeş-Bolyai University, Cluj Napoca, Romania) from the Upper Cretaceous Şard Formation (= middle section of the Sebeş Formation) (Transylvanian Basin, Romania) as a pterosaur premaxillary cranial crest. They assign this fossil to a new species of small pterosaur, *Thalassodromeus sebesensis* (a name first coined in a conference abstract published in 2013; Grellet-Tinner et al., 2013). GTC build a taxonomic argument on the basis of this single incomplete specimen that posits the presence of a major group of pterosaurs hitherto entirely restricted to the Early Cretaceous of South America - thalassodromines (Kellner and Campos, 2007) or thalassodromids (Witton, 2009) - in the European Late Cretaceous. GTC note that "this important discovery doubles the thalassadromine fossil record and demonstrates a 42 million years temporal displacement between the Romanian species and its older Aptian Gondwanan congener *Thalassodromeus sethi*". If GTC are correct, this new fossil represents a remarkably unexpected and potentially very important discovery that could rewrite aspects of pterosaur evolutionary history.

We have assembled a large international team who disagree with the arguments presented by GTC. As we demonstrate, the fossil fragment they describe is misidentified; it is, firstly, not from a pterosaur but is clearly a piece of the shell of the turtle *Kallokibotion* Nopcsa, 1923 and, secondly, is therefore not the groundbreaking discovery of an 'anachronistic' Gondwanan pterosaur in Europe as claimed. Because ODA-28 is not a pterosaur, yet alone a *Thalassodromeus*, GTC's conclusions on migration routes and insular dwarfism are also unsupported.

2. ODA-28 is not a pterosaur head crest or even part of a pterosaur

The similarity of ODA-28 to pterosaur fossils is superficial; the GTC specimen possesses no apomorphies or other characteristic features of Pterosauria. Most importantly, the thickness, cross sectional morphology, and asymmetry of the specimen demonstrate that it is not a pterosaur head crest, or a pterosaur bone of any kind. Pterodactyloid bones, including the head crests and bones of thalassodromines, are characterised by millimetre-thick bone walls separated by networks of fine trabeculae (e.g. de Ricqlès et al., 2000, Sayão, 2003, Steel et al., 2005, Fig, 4; Steel, 2008). In contrast, broken margins of ODA-28 exhibit two layers of compact bone separated by a diploë (a a spongy layer), not thin bone separated by trabeculae. In ODA-28 the two compact bone layers are asymmetrical, with one layer thicker than the other. Pterosaur cranial crests, on the other hand, are medially positioned structures with symmetrical bone thickness on the left and right sides (Kellner and Campos, 2002; Martill and Naish, 2006).

The anatomy of ODA-28 is distinctly different from all known pterosaur head crests. The 'fossae' meant to link ODA-28 to *Thalassodromeus sethi* are morphologically and topographically unlike the fenestrae at the base of *Thalassodromeus* headcrests, which are elongate, located posterior to the orbit (and thus to the nasoantorbital fenestra), and perforated (Kellner and Campos, 2007, Fig. 10). Alleged anatomical features of the specimen, including a nasal process, anterodorsal margin of the nasoantorbital fenestra, and 'finger-like projections' from alleged crest margins, are morphologically irreconcilable with thalassodromines and other pterosaur crania and are, as we will demonstrate below, consistent with identification of this material as part of a turtle.

Even if ODA-28 unexpectedly represents a histologically and morphologically bizarre pterosaurian bone, it does not exhibit any clear similarities with the pterosaur *Thalassodromeus*. For example, the irregular 'ventral' margin of ODA-28 compares poorly with the smooth, sweeping nasoantorbital margin of *Thalassodromeus* and other

monofenestratan pterosaurs (Martill and Naish, 2006, Kellner and Campos, 2007). The flat, unremarkable 'nasal process' of ODA-28 is entirely unlike the tapering process of the nasal of *Thalassodromeus* and related pterosaurs. The "finger-like projections" of ODA-28 are not seen in *Thalassodromeus*, and in fact have no precedent on any pterosaur cranial crest, even among the fine, fibrous crest structures which anchored soft-tissues in many pterosaur species (e.g. Frey et al., 2003).

3. ODA-28 is a piece of fossil turtle shell

In the Supplementary Text accompanying their paper GTC discussed (and rejected) the possibility that ODA-28 might be part of a turtle. This is the correct interpretation of this fragmentary specimen; ODA-28 is a partial posterior plastral lobe of the turtle *Kallokibotion* Nopcsa, 1923. Specifically, this specimen is an articulated left hypoplastron and xiphiplastron with a damaged inguinal buttress and a partially broken anal notch, preserved in a sandstone concretion and exposed in dorsal/internal view (Fig.1). Our reinterpretation is based on several morphological characters discussed below and comparison with the posterior plastral elements of other *Kallokibotion* specimens, including the designated type material (Nopcsa, 1923b; Gaffney and Meylan, 1992).

The hypoplastron is trapezoidal and exhibits a well-developed sutural margin on its cranial edge (the mesoplastron/hyoplastron-hypoplastral contact), as in *Kallokibotion*. Based on the diverging angle of the meso-hypoplastral suture, we suspect that originally the two mesoplastra were not in contact axially (as in *K. bajazidi*) (so there is also hyoplastron-hypoplastron contact medially). What GTC identified as "finger-like projections" represent incomplete ossification of the inter-hypoplastral sutures, as is characteristic of juvenile and sub-adult individuals. The inguinal buttress (where the maximum bone thickness is reached)

is distally incomplete, and extends laterally from the long axis at a right angle, forming what GTC identified as the "posterior margin of the nasoantorbital fenestra".

The xiphiplastron is triangular in shape. The suture between the hypoplastron and xiphiplastron is clearly visible on ODA-28, with a process on the xiphiplastron close to the lateral edge fitting into a notch on the hypoplastron, as in other turtles. Among its most striking features are the posterolateral skin sulcus (identified by GTC as the "nasal process"), which in most turtles represents the attachment margin of the skin (body-wall), and the pubic attachment area (identified by GTC as the "fossa"), where the lateral pubic process is attached to the plastron by ligaments. This attachment site is often present in stem-turtles and some cryptodires (in pleurodirans the contact is sutural) (see for e.g. *Proganochelys*, meiolanids and *Glyptops*; Gaffney, 1990). In *Kallokibotion* the pubic articular facet is present on the centro-lateral part of the xiphiplastron and is oval or subrounded in shape (Natural History Museum, London; NHMUK R4930), nearly identical in shape, size, and position to the 'fossa' on ODA-28 (Fig. 1).

ODA-28 also exhibits several other uncanny similarities with *Kallokibotion* and other turtles. The visceral (=dorsal) surface of the hypo-xiphiplastron is generally smooth but exhibits a series of fine lineations, which are especially concentrated close to the inguinal process, along the sutural margins and radiating around the pubic articular facet. This specific type of plastron texture is common in many turtles and marks both soft tissue attachments and a small degree of surface vascularization. Additionally, features identified by GTC as the "trabecular" internal structure of the bone (clearly distinct from the condition present in pterosaur cranial crests; see above) is common in turtles and usually formed by a highly vascularized external cortex, an extensive interior cancellous area formed by short and thick trabeculae, and a relatively thin, fibrolamellar internal cortex.

The morphology of the hypoplastron and xiphiplastron, and in particular the size and shape of the inguinal buttress, the orientation of the meso-hypoplastral suture (indicating the presence of a wide triangular mesoplastron), the development of the xiphiplastral skin sulcus, and the size and position of the pubic articular facet, clearly indicate referral of ODA-28 to the turtle *Kallokibotion*, and it is a perfect match to NHMUK R4930, the lectotype of *Kallokibotion magnificum* Nopcsa 1923 (Fig 1) (this species was synonymised with *K. bajazidi* by Gaffney and Meylan, 1992; see Rabi et al., 2013).

4. Evolutionary implications

Based on their incorrect identification of ODA-28 as a pterosaur crest, GTC built a classic 'house of cards' scenario: the misidentification of one fragmentary fossil leading to a cascade of elaborate ideas with increasingly far-reaching implications. These include bizarre and implausible soft-tissue and ecological hypotheses: e.g. the crest anchored muscles and a 'sizeable fleshy crest' and acted as a rudder in flight; this supposed new pterosaur demonstrates hitherto unappreciated co-evolution between Romanian pterosaurs and angiosperms, and; the hypothesis that their new taxon supports ecological segregation between azhdarchids and thalassodromines. None of these hypotheses are supported now that ODA-28 is identified as a turtle.

5. Conclusions

The new Romanian fossil ODA-28 described by GTC shares no apomorphic characters with pterosaurs, lacks the microstructure and anatomical features of pterosaur head crests, and shares numerous features with *Kallokibotion* and other turtles. We therefore reassign ODA-28 to the common Upper Cretaceous European turtle *Kallokibotion*. Additional preparation and study of ODA-28 is almost certain to corroborate our re-identification. We

predict that histological thin sectioning will demonstrate characteristic turtle, not pterosaur, internal texture and vascularization patterns. We also predict that preparation of the other side of ODA-28 will reveal the fine vermicular texture and sulci for the dermal scales across the hypoplastron and xiphiplastron, as is characteristic for turtles and which clearly would not be present in a pterosaur. Finally we predict that preparation or CT scanning of the embedded side will reveal the full asymmetric three-dimensional morphology expected for a turtle plastron but not for a symmetrical pterosaur head crest. We are currently not able to perform these analyses, as the specimen is inaccessible to us (V. Codrea, pers. comm. to G. Dyke, July 2014), but look forward to the additional data GTC will bring on this intriguing fossil. The name *Thalassodromeus sebesensis* Grellet-Tinner and Codrea, 2014 should be synonymised under *Kallokibotion bajazidi*.

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Figure Caption

Fig. 1. The turtle affinities of ODA-28. (A) NHMUK R4930, the lectotype plastron of *Kallokibotion magnificum* Nopcsa 1923, with the portion corresponding to ODA-28 outlined in black (photo supplied by S. Chapman, Natural History Museum, London). (B) ODA-28 (modified from Grellet-Tinner & Codrea, 2014). Abbreviations: hypo, hypoplastron; hxc, hypoplastron-xiphiplastron suture; ihc, intra-hypoplastral suture; ib, inguinal buttress; ps, pubic scar; meso, mesoplastron; mhc, meso-hypoplastral contact; pll, posterolateral lip; xiphi, xiphiplastron. Scale bar for A equals 5 cm.

Fig.1

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